Environmental heterogeneity and dispersal processes influence post-logging seedling establishment in a Chiquitano dry tropical forest

Robin Corrià-Ainslie[1,2*], J. Julio Camarero[1,2] and Marisol Toledo[2, 3]

[1]Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas (IPE-CSIC). Avda. Montañana 1005, Apdo. 202, E-50059 Zaragoza, Spain.

[2]Instituto Boliviano de Investigación Forestal (IBIF), PO Box 6204, Santa Cruz de la Sierra, Bolivia.

[3]Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Km 9 al norte, El Vallecito, Santa Cruz de la Sierra, Bolivia.

*Corresponding author:
R. Corrià Ainslie
Instituto Pirenaico de Ecología (IPE-CSIC)
Avda. Montañana, 1005
50059 Zaragoza, Spain.
E-mail: rcorria@ipe.csic.es
Tel.: (+34) 976 716031, Fax: (+34) 976 716019

Abstract

Selective logging is becoming more and more influential in forest use in the tropics, especially as it provides local communities and regions with timber resources. Logging greatly alters abiotic and biotic factors which are fundamental in seedling establishment and spatial heterogeneity of tree recruitment. Niche and dispersal processes may affect post-logging seedling establishment, particularly in water-constrained tropical dry forests (TDF). To understand how selective logging affects tree recruitment and how forest exploitation can become a sustainable practice; a theoretical framework has been set up based on these processes. We assessed post-logging seedling establishment in a Bolivian Chiquitano TDF by: (i) characterizing logging microsites and the variability in abiotic (canopy openness, soil compaction and soil water content) and biotic (short and long-distance dispersal) factors among them, (ii) evaluating the roles played by those factors, here considered surrogates of niche and dispersal processes, on seedling establishment, and (iii) providing guidelines to ensure tree regeneration in similar logged TDFs. One year after logging, seedling establishment of five canopy tree species was assessed in four microsite types created by selective logging and in undisturbed TDF. Dispersal processes were described by interpolated kernel estimates of abundance of adult trees, i.e. potential seed sources. After logging, the abiotic environment was considerably altered, especially in the most disturbed logging microsites, leading to significant changes in canopy openness and soil compaction, the most important factors determining seedling establishment in four out of the five studied species. Dispersal processes also influenced regeneration in three tree species. Since the spatial distribution of adult trees influences post-logging regeneration, this should be considered to improve sustainability in logging operations across the tropics.

Key words: environmental heterogeneity, tropical dry forest, soil compaction, canopy openness, zero-inflated Poisson models.

Introduction

Environmental heterogeneity is one of the most important mechanisms favouring species coexistence in tropical forests (Wright, 2002), which are among the most diverse ecosystems on earth (Myers et al., 2000). They are subjected to profound land-use changes (Wright, 2010) and face a massive loss of biodiversity (Dirzo and Raven, 2003). Within the tropical biomes, Tropical Dry Forests (TDF) are threatened by the expanding agricultural border, since they develop on fertile soils, therefore only a very small portion of them remain unaltered (Pennington et al., 2006).

Whereas deforestation and diversity are major consequences of abandoned agriculture, pasture expansion and tree plantations, selective logging is a much less disturbing practice (Gibson et al., 2011) but is increasing its extension in tropical areas (Asner et al., 2005). Moreover, reduced impact logging, can be seen as a strategy to reduce the use pressure on TDFs (Fredericksen and Putz, 2003), while offering viable economic alternatives to local communities in developing tropical regions (Merry et al., 2009). This management technique reduces canopy and ground disturbance by more than half compared to conventional selective logging (Pereira Jr. et al., 2002).

Selective logging causes a reduction of stand basal area and damages neighbouring trees, particularly those forming subcanopy layers, while affecting soil conditions (Asner et al., 2005; Johns, 1988). As a result of logging abiotic conditions suffer negative alterations (e.g., erosion, run-off, microclimate). Biotic interactions are also changed due to modifications in the availability of resources to plants (Clark and Covey, 2012). For instance, logging increases light availability and temperature, decreases relative air humidity (Johns, 1985), changes rooting environments (Fredericksen and Pariona, 2002), and enhances the development of understory

vegetation (Fredericksen and Mostacedo, 2000). Therefore, selective logging increases environmental heterogeneity by creating spatiotemporal variation in the distribution of abiotic resources and creates regeneration niches for tree recruitment (Denslow, 1980; Grubb, 1977). These two processes are considered among the main mechanisms explaining tree species coexistence in tropical forests (Wright, 2002). Natural treefall gaps also play a key role in maintaining spatial heterogeneity in the composition and dynamics of tropical forests (Brokaw, 1985) by generating microsite heterogeneity in the distribution of abiotic resources, which determines the regeneration success of each tree species (Rother et al., 2013).

Abiotic factors related to the dry season play a far-reaching role not only in tree regeneration but in overall dynamics (Ceccon et al., 2006; Comita and Engelbrecht, 2009; Powers et al., 2009). Seasonality in the availability of water is an important driver of growth, reproduction and survival patterns in TDFs (McLaren and McDonald, 2005; Mendivelso et al., 2013; Murphy and Lugo, 1986). Whereas in wet tropical forest the tree regeneration dynamics are directly related to light availability in the understory, in TDFs the relationship is considered to be less relevant (Chazdon et al., 1996; Rozendaal et al., 2006). Drought creates a more open canopy structure, given the deciduous habit and the compound leaf structure of the most abundant trees (Killeen et al., 1998; Murphy and Lugo, 1986). It is to a large extent the ability of each species in TDFs to tolerate distinct levels of light irradiance and water availability that channels the response of seedling establishment to changing abiotic resources (Rozendaal et al., 2006; Poorter and Markesteijn, 2008a).

In TDFs the dominance of wind dispersed trees over animal and gravity-dispersed trees also determines seed dispersal processes and seedling establishment (Bullock et al., 1995; Lebrija-Trejos et al., 2008). Another important mechanism

101 favoring species coexistence is recruitment limitation. This process, depending on
102 species dispersal syndromes and requirements for seedling establishment, occurs if
103 seeds of a species do not reach available microsites for regeneration (Wright, 2002).

104 There is a need to increase our knowledge about regeneration niches of many
105 TDF tree species since these are among the most threatened types of tropical forests
106 (Ceccon et al., 2006; Fredericksen and Mostacedo, 2000). The existence of unknown
107 biotic factors involved in tree regeneration processes, besides environmental factors,
108 may led to an important portion of variance in the results unexplained (Fredericksen and
109 Pariona, 2002; Park et al., 2005). Therefore, we used a spatially explicit model to gain
110 insights into the niche and dispersal processes influencing seedling regeneration after
111 selective logging of a TDF. We selected a forestry concession for selective logging
112 located in the Chiquitano forest, in the Bolivian lowlands, a type of TDF that has long
113 been threatened and stated as a global conservation priority (Parker III et al., 1995). We
114 analized the distribution of seedlings and resprouts of the most abundant timber tree
115 species one year after selective logging in order to: (i) describe logging microsites and
116 the variability in biotic and abiotic microsite variables; (ii) evaluate the role of abiotic
117 factors (canopy opening, soil disturbance), and dispersal processes on seedling
118 establishment; and (iii) provide guidelines to improve management in order to ensure
119 seedling establishment in logged TDFs.

120

121 **Materials and methods**

122 *Study site*

123 This study was conducted in a Chiquitano TDF located in the eastern lowlands of
124 Bolivia. It has a distinct dry season of five months, from May to September, where
125 precipitation is below 100 mm. Meteorological data obtained from the Concepción

126 station (16° 15’ S, 62° 06’ W; data available for the period 1949–2009; station located
127 35 km away from the study site) show that mean annual temperature is 24.3 °C and
128 mean annual rainfall is 1177 mm. The terrain in the site is typical of the Brazilian
129 Shield, with rolling hills of Precambrian origin located between 300 and 550 m a.s.l.
130 and superficial, reddish-brown inceptisols and oxisols.

131 The Chiquitano forest is located in the transition between the dry Chaco in the
132 south and the humid Amazon Basin in the north. It is probably the largest remaining
133 patch and one of the most floristically diverse TDF in the Neotropics(Killeen et al.,
134 1998; Parker III et al., 1995). Floristically it is considered a distinct floristic region from
135 the Chaco and the Amazonian forest (Killeen et al., 2006), but with few endemic
136 species. The forest structure is characterized by an open 25-35 m tall canopy allowing
137 the development of a high density of sub-canopy trees, shrubs and lianas (Killeen et al.,
138 1998). There are locally abundant ground bromeliad species that can occupy most of the
139 forest floor. Most canopy trees species are deciduous or semi-deciduous, while most
140 sub-canopy tree species are evergreen (Justiniano and Fredericksen, 2000).

141 The study site is located in a 30,000 ha forest concession for sustainable
142 management (INPA Parket company; 16º 07’ S, 61º 43’ W, 380 m a.s.l.) located near
143 Concepción, Santa Cruz Department. Roughly 10 % of the total area is a reserve, and
144 permanent sample plots are monitored regularly by the Instituto Boliviano de
145 InvestigaciónForestal (IBIF), a non-governmental forest conservation and research
146 agency. Before logging operations begin a forest census is carried out, where
147 commercial timber tree species above 40 cm at breast height (DBH, diameter measured
148 at 1.3 m) are mapped and tagged. Approximately, 20 % of the mapped individuals are
149 left for seed production. The minimum cutting cycle in INPA is 25 years according to
150 the Bolivian forestry law.

151

152 *Sampling design*

153 We selected areas with distinct post-logging light and rooting environments and defined
154 five microsite types, four of them created by selective logging. In order to compare
155 these microsites with forest areas not affected by logging, undisturbed forest microsites
156 were selected (Fig. 1). Logging microsites included logging roads, log landings, skid
157 trails, logging gaps and undisturbed forests, each with differing soil and canopy
158 disturbance intensities. Undisturbed microsites had high canopy cover and no soil
159 disturbance. To avoid site effects caused by environmental heterogeneity (soil,
160 topography, etc.) we used a block sampling design with the five aforementioned
161 microsite types in each block taking the log landing as the epicentre of each block. We
162 established 24 blocks in two different study areas. These areas covered 600 and 1000
163 ha, respectively. The first block number was given to the log landings, the least
164 abundant microsite types, after searching thoroughly within the two study areas. Then,
165 we located the rest of logging microsite types with a minimum distance of 50 m
166 between them.

167

168 *Measured variables*

169 In July 2012, one year after selective logging, 120 square plots (2 x 2 m) were set out at
170 the five microsite types, i.e. 24 plots per microsite. An undisturbed forest plot was also
171 located in the nearest undisturbed forest fragment, located at least 50 m away from the
172 disturbed microsites to reduce effects due to positive spatial autocorrelation. All plots
173 had their location noted with an approximate resolution of 10 m based on GPS
174 measures, which we assume would impact similarly the interpolated kernel density
175 values across the study plots. In logging roads and skid trails we measured the width of

176 the road, while in logging landings and logging gaps we measured the length of the two
177 major perpendicular axes and calculated their areas assuming they were ellipses. At the
178 four corners of each plot we measured soil compaction (in N m^{-2}) with a hand
179 penetrometer (Eijkelkamp, Giesbeek, the Netherlands) and volumetric soil water
180 content (%) in the upper soil layer (10 cm) using a TDR probe (Theta Probe Soil
181 Moisture Sensor, Delta-T, Cambridge, UK). Canopy openness (%), i.e. the area not
182 covered by the canopy, was measured at the center of each plot with a spherical
183 densitometer (Stumpf, 2008). Percent cover of trees, shrubs, woody vines, herbaceous
184 vines and herbs or forbs was estimated in each plot. We proceeded to the identification
185 of species together with a census of all newly emerged seedlings and resprouts of the
186 most abundant canopy tree species within the plots. We differentiated seedling from
187 resprouts by looking for cotyledon scars only present in seedlings.
188
189 *Determining seed sources and distances from adult trees*
190 Prior to selective logging in 2011, forest censuses of the timber tree species were carried
191 out by the INPA company and the IBIF. In those censuses, every tree with a DBH > 40
192 cm was identified to species and mapped. We used mapped tree populations from the
193 commercial censuses to calculate kernel density maps of the three most abundant timber
194 tree species. In this way, we obtained a quantitative estimate of seed sources in the
195 study area, with reference to potential 'mother' trees capable of reaching a reproductive
196 size or age. Those maps represented interpolated intensity values, i.e. the mean number
197 of points per unit area (tree density).
198 We used two different criteria for bandwidth selection to build two kernel
199 density maps of the most abundant species: one with a lower bandwidth and the other
200 with a higher bandwidth. This allowed us to consider each species density map as a

surrogate of density of seed sources under two scenarios: short- (SDD) and long-distance dispersal (LDD), respectively. Using tree species as a mark, we started off by creating a marked point pattern with the two censuses. A kernel density map of each species was then calculated in order to select the two dispersal scenarios. This step involved the use of a function where the effects of intensity variation can be separated from the effect of clustering in heterogeneous point processes (Baddeley and Turner, 2005; Diggle, 1985). This produced a value of sigma (the smoothing bandwidth parameter) for all tree species between 40.69 and 66.25 m in the 600 and 1000-ha large areas, respectively. For the higher bandwidth, we did the kernel density map for each species separately, applying a common bandwidth with information from each species (Baddeley and Turner, 2005; Kelsall and Diggle, 1995), which returned a value of sigma of 149.49 and 188.55 m in the 600 and 1000-ha large areas, respectively. Then for each species we obtained the density of potential seed sources at each plot by sampling the kernel maps at the coordinates of the 120 plots. It is important to note that the density of seed sources in each sampled plot is based not only on the adult trees nearby but also on the whole adult tree population.

Statistical analyses: zero-inflated Poisson mixed models

Using the package *agricolae* in the R statistical package (R Core Team, 2013), we conducted Kruskal-Walis tests to test for differences in the biotic and abiotic variables between logging microsites and also to test if seedling establishment differed between microsites.

The next step was to evaluate the role played in seedling establishment by factors such as the abiotic variables, the competition with resprouts of selected tree species and the dispersal processes. Since establishment data followed a zero-inflated

Poisson distribution we applied zero-inflated generalized linear mixed models with a Poisson distribution (referred throughout the text as zero-inflated Poisson mixed models; Zuur et al. 2012). Using seedling density (individuals m^{-2}) as a response variable, we conducted a set of models, with soil compaction, canopy openness, soil water content, vegetation cover, resprout abundance and density of seed sources (both SDD and LDD data) as explanatory variables. Since our response variables are counts and contain more zeros than expected by the Poisson distribution, they follow a zero-inflated Poisson distribution (Zuur, 2009). Therefore, we used a zero-inflated Poisson model (Zuur et al. 2012) where the zeros are classified differently. The structural or true zeros refer to the absence of a species in the plot due to the unsuitability of the conditions in the plot. On the other hand, the false or sampling zeros are caused by errors in design, sampling or observation. Hence, some zeros were included in a binomial model to model the probability that a zero value is observed (zero vs. non-zero values), and some zeros were modeled with a Poisson model including all counts (zeros and positive values).

In the exploratory analysis prior to this, after checking for collinearity between the explanatory variables by calculating the variance inflation factor (VIF), weremoved those variables with VIF > 3 (Zuur et al., 2010). Highly correlated variables such as tree and shrub percent cover were also removed, whereas canopy openness and soil compaction were retained, since these are two correlated variables which relate to different physical processes.

Before fitting the models we standardized all explanatory variables, so they all had mean of zero and standard deviation of one. We used the *glmmADMB* package (Fournier et al., 2012; Skaug et al., 2012) to fit zero-inflated Poisson mixed models in the R statistical package (RCore Team, 2013). Each model included a Monte Carlo

procedure, run with 50000 iterations, to obtain samples from a posterior distribution of the model parameters in order to find confidence intervals (Zuur et al., 2012).

To check for the presence of spatial autocorrelation in the response variable (seedling density) we calculated spline correlograms of the raw establishment data and used the bootstrap method (1500 replications) to calculate 95% confidence envelopes (BjØrnstad and Falck, 2001). Furthermore we also calculated spline correlograms of the Pearson residuals of the zero-inflated Poisson mixed models to inspect whether some spatial autocorrelation remained after accounting for the spatial autocorrelation of the explanatory variables (Zuur, 2009).

Finally, we generated a series of alternative zero-inflated Poisson mixed models for every species with different combinations of the explanatory variables. All models were ranked according to the Akaike Information Criterion (AIC). We calculated the Akaike weights (*Wi*) -the relative probability of each model being the best- and established the 95% confidence set of models (Zuur, 2009). To calculate the relative importance of each variable, we used the sum of the Akaike weights of all models where that specific variable was found.

Results

Selective logging

Selective logging removed 8550 trees of 16 timber tree species, and 77% of those trees had DBH > 40 cm. On average 5.29 individuals ha^{-1} and 7.56 m^3 ha^{-1} in volume were removed. Consequently, numerous logging microsites were created, differing in area, soil and canopy disturbance and vegetation cover (Fig. 1, Table 1).

Log landings occupied significantly larger areas than logging gaps ($W = 437$, $P < 0.0001$; see Table 1). Log landings showed the highest soil and canopy disturbance,

followed by logging roads, skid trails and log gaps, the latter microsites showing partial soil disturbance and moderate canopy disturbance. Logging landings presented the highest soil compaction and high canopy openness, whereas logging roads had similarly high soil compaction and lower canopy openness (Table 1, Fig. 2). Skid trails had lower soil compaction and canopy openness while logging gaps had low soil compaction and intermediate canopy openness. The undisturbed sites had the lowest canopy openness and the second lowest soil compaction. Soil water content significantly differed between microsites (ANOVA, $F = 3.58$, $P = 0.009$) with logging landings showing the maximum value (Table 1).

Seedling establishment

We found 360 recently-emerged seedlings in the sampled plots, corresponding to 20 tree species. Among the five most abundant tree species (Table 2), *Acosmium cardenasii* was the most abundant, followed by *Machaerium acutifolium*. The rest of species had similarly lower seedling densities. As in the case of *Centrolobium microchaete* and *Tabebuia impetiginosa*, some species appeared mainly as resprouts rather than seedlings. *A. cardenasii*, the most abundant species, also had an important number of resprouts, as had three of the studied species (Table 2).

Seedling establishment in all five main tree species differed between logging microsites (Fig. 3). In *A. cardenasii* establishment was very low in highly disturbed microsites (e.g., log landings and roads), but high in undisturbed forest. In the case of *Caesalpinia pluviosa* there was no establishment in the most disturbed microsites, establishment was low in intermediately disturbed microsites (e.g., logging gap, skid trail) and much higher in undisturbed forest. Similarly, in *M. acutifolium* establishment was very low in disturbed microsites and high in undisturbed forest. On the other hand

Anadenanthera macrocarpa did not establish in undisturbed forest, while its establishment was high in logging gaps. Lastly, *Astronium urundeuva* established successfully in logging roads and skid trails.

Density of adult trees

The Kernel density maps of the three selected tree species revealed how density of seed sources varied across both study areas for each species (Figs. 4 and 5). The different bandwidth selection methods showed how density changed as a surrogate of short- and long distance-dispersal from the adult "mother" trees. The estimated densities of seed-source trees for the 600- and 1000-ha large study areas were, respectively, 2.10 and 1.48 ind ha^{-1} for *A. macrocarpa*, 0.11 and 0.04 ind ha^{-1} for *C. pluviosa* and 0.49 and 0.08 ind ha^{-1} for *A. urundeuva*.

Niche and dispersal effects on seedling establishment

In four out of five tree species, models including niche variables were the best predictors of seedling establishment (Tables 3 and 4). Both *A. cardenasii* and *M. acutifolium* were influenced by niche variables, whereas *A. macrocarpa* and *C. pluviosa* were significantly influenced by niche variables and by dispersal processes together, and *A. urundeuva* was only influenced by dispersal processes (Table 4).

Regarding the two species whose establishment was only related to niche variables, *A. cardenasii* establishment decreased significantly with soil compaction and canopy openness, while *M. acutifolium* preferably established in microsites with closed canopies (Tables 3 and 4; see also Fig. 6). In the case of species whose establishment was linked to niche and dispersal variables, *A. macrocarpa* establishment increased significantly with increasing canopy openness, while it augmented with increasing

short-distance seed dispersal (Table 4; Fig. 6). In the case of *A. urundeuva* establishment increased with increasing dispersal over long distances (Fig. 6), while the rest of variables played a minor role. Finally, *C. pluviosa* establishment decreased as canopy openness and soil compaction increased, while it increased in response to dispersal over short distances (Fig. 6).

Discussion

Effects of logging on environmental heterogeneity

Logging intensity in the study area was lower than in other exploited TDFs (Baraloto et al., 2012; Villela et al., 2006) and nearby humid tropical forests (Fredericksen and Pariona, 2002; Peña-Claros et al., 2008), and much lower than the average selective logging intensity of 23 m^3 ha^{-1} applied in some sites of the Amazon Basin (Asner et al., 2005; Pereira Jr. et al., 2002). This relatively low logging intensity is consistent with the lower basal area, canopy height and growth rates of TDFs as compared to wet tropical forests. As we expected, this led to a clear gradient of canopy and soil disturbances.

Logging landing, characterized by very open canopies and highly disturbed soils (soil scarification and compaction) emerged as the most disturbed microsite. Logging roads, with similar soil conditions but lower canopy disturbance, was the second most disturbed microsite. Skid trails had intermediate soil disturbance and little canopy disturbance, while logging gaps presented low soil disturbance and higher canopy disturbance. In undisturbed sites, soil compaction may be increased as a result of the dense network of roots often found in such sites. This could be an explanation for the higher values of soil compaction in undisturbed sites in comparison to that of logging sites. These results are in accordance with the findings of Fredericksen and Mostacedo (2000) six months after logging in another Chiquitano dry forest site. They found

significant differences in tree cover in the most disturbed logging landings and roads, in comparison to the least disturbed logging gaps and undisturbed microsites. They also found soil disturbance was much higher in logging landings and gaps than in the rest of logging microsites. Fredericksen and Pariona (2002) also reported that scarified areas varied across logging gaps in a nearby humid tropical forest in Guarayos, Santa Cruz.

Effects of environmental heterogeneity on seedling establishment

After logging, the abiotic environment was considerably altered, especially in the most disturbed logging microsites, leading to changes in light, soil moisture and rooting conditions, which are important factors determining seedling establishment (Oliver and Larson, 1996).

High canopy openness significantly reduced the establishment of three tree species (*A. cardenasii*, *C. pluviosa* and *M. acutifolium*), and affected recruitment of all species. Overall average seedling establishment was low, with *A. cardenasii*, *A. macrocarpa* and *M. acutifolium* showing the highest values. This is consistent with the relative abundances of these species found by the Long Term Silvicultural Research Program (LTSRP) plots monitored every 2-3 years in INPA by IBIF since 2002, with these species ranked, respectively, as first, second and fifth (unpublished data). These abundances were also similar to the ones found in another Chiquitano forest in the Lomerio site (Fredericksen and Mostacedo, 2000).

Functional groups of species with distinct ability to regenerate under different light conditions (Poorter et al., 2006), have been reported to respond differently to selective logging (Arets et al., 2003; Berry et al., 2008; DongKai et al., 2010). The observed differences in seedling establishment were in agreement with the characteristic shade tolerance of the species guilds (Table 2). The shade-tolerant *A. cardenasii* and the

partially shade-tolerant *C. pluviosa* and *M. acutifolium* showed similar patterns of decreasing seedling establishment with logging disturbance, mainly due to the differences in light availability and also in soil compaction. Accordingly, the long-lived-pioneers *A. macrocarpa* and *A. urundeuva* had the highest establishment in intermediately disturbed microsites. These results indicate that logging causes an increase in the abundance of pioneer and mid-tolerant species. As for the shade-tolerant species, they remain dominant in undisturbed forest (DongKai et al., 2010; Peña-Claros et al., 2008).

Abundance of pioneer species also decreases with increasing time since logging in sites logged long time ago (Verburg and van Eijk-Bos, 2003). Similarly we can refer to another Chiquitano TDF study near our study site. The establishment of *A. macrocarpa* and *A. urundeuva* was higher in the most disturbed sites one year after selective logging, while *C. pluviosa* had similarly high establishment in the least disturbed sites (Fredericksen and Mostacedo, 2000). Similar responses have been found in a dipterocarp forest in Borneo, where pioneer species were dominant in logged forests, suggesting successful establishment shortly after logging (Berry et al., 2008). In a Bolivian wet tropical forest soil scarification due to skidder disturbance had some positive effects in seedling density (Fredericksen and Pariona, 2002), although other unknown factors influenced seedling establishment. In the same site pioneer species dominated establishment in recent gaps, although some timber tree species also ended up dominating logging gaps (Park et al., 2005). Moreover, functional guilds also show different growth rates in response to disturbance. In the INPA site it has been found that the increase in growth rates due to silvicultural treatments is higher in pioneer than in shade-tolerant tree species (Villegas et al., 2009).

Taking into account the differences found in soil water content among logging microsites, we found the effect of soil water content on seedling establishment to be insignificant. The importance of soil water content in explaining tree recruitment was low as compared to other abiotic factors as canopy openness or soil compaction. This could be due to the shallow soil layer considered or to the period when soil water content was measured. Although soil water content was measured during the dry season, the availability of local soil water could have been altered notably after a few rainy days. Moreover, soil water availability could also be affected by differences in soil texture, depth and organic matter content in the logging microsites.

There is a contrast between these results and other studies. Drought intensity and water availability have been seen to play a major role in the distribution of plant species in moist tropical forests (Engelbrecht et al., 2007; Condit et al., 2013). The reason for such contrasting results could be the difference in the scales used in each study and the types of forests compared. Their calculations were based on tree drought sensitivity, which is the relative difference in seedling survival over the dry season, comparing dry plots to experimentally irrigated ones. This information was then related to the regional and local abundance of each species. In contrast to this method, in our study we estimated shallow soil water content as an on the spot reference to water availability and related it to local seedling abundance. There are, of course, differences in the annual precipitation, which is much lower at INPA than in Barro Colorado Island (2612 mm), where these studies were performed (Windsor, 1990). One final point to bear in mind is the influence of seedling traits in drought survival (Poorter and Markesteijn, 2008b). These traits could buffer soil conditions and be of long-lasting importance in determining a species regeneration niche (Poorter, 2007).

Dispersal effects on seedling establishment

Seed dispersal is considered to be fundamental in determining recruitment and expansion rates in tree species particularly at large spatial scales (Nathan and Muller-Landau, 2000). To study the effect of dispersal from parent trees on seedling establishment we estimated seed rain. We did so using kernel density maps of adult trees, as we considered adult trees as density of seed sources a surrogate of seed rain. The heterogeneous patterns of the kernel density maps suggested that the distribution of some of the study tree species could related to dispersal limitation when the availability of seeds is limiting recruitment at the landscape level (Münzbergová and Herben, 2005).

Density of seed sources and location of adult reproductive trees played an important role in seedling establishment in three out of the five study species. The relative importance of dispersal and niche factors in seedling establishment (Table 3) could be directly related to the availability of seeds (seed limitation) and the availability of suitable microsites (establishment limitation), respectively. For instance, in *A. macrocarpa*, the availability of seeds, when compared with the availability of suitable microsites, revealed similar contributions on seedling establishment. However, our inferential analyses should be complemented with additional data on fruit production and seed censuses to strengthen our conclusions. Furthermore, the location of adult reproductive trees could be a legacy of past events including logging or fires.

In *A. urundeuva*, seed limitation contributed much more whilst in *C. pluviosa* establishment limitation had a greater effect on seedling establishment. Our results suggest that effective regeneration can be fulfilled through different pathways modulated by biotic and abiotic factors and their interactions (Pulido et al., 2010).

Implications for the management of logged tropical dry forests

450 The low logging intensity in the study site in terms of individuals harvested per area
451 could be considered high if the overall damage caused per logged tree is taken into
452 account (Panfil and Gullison, 1998). Nevertheless, we consider that harvest intensity in
453 the study site is already optimized to cause little residual damage, i.e. damage to non-
454 logged trees. This research provides further understanding of the specific environmental
455 and biotic constrains of tree recruitment as the dominant roles played by canopy
456 openness and soil compaction in the study TDF. This knowledge would lead to a deeper
457 understanding of the reasons for regeneration success or failure in some commercial tree
458 species after logging. Silviculture management techniques based on species guilds (Park
459 et al., 2005) are essential in this context. Examples of the negative effects of
460 overharvesting can be seen in the INPA forest and in other Neotropical TDFs, where
461 some of the most valuable timber tree species have been depleted (Gullison et al., 1996;
462 Grogan and Galvão, 2006). Careful management is needed to restore these forest stands
463 to be sustainable. Therefore our management recommendations are to carefully plan
464 logging operations species by species according to local abundances and the knowledge
465 of their recruitment strategies after logging disturbance.

466 Moreover, the results in our study make it clear that the way to guarantee
467 adequate regeneration of some timber tree species is by focusing on the spatial
468 distribution of the adult trees which represent future harvestable trees. This information
469 can be used to detect areas where local abundance of a species is high enough for
470 adequate regeneration. Rather than harvesting a species only if the harvestable
471 individuals attains a minimum density threshold on average on a large enough area
472 (e.g., 600 ha), we also suggest using size thresholds on smaller areas (5-10 ha) that take
473 into account the local variations in density of seed sources. This is especially important
474 for species with heterogeneous spatial distributions either caused by spatial

475 heterogeneity in the distribution of abiotic resources (slope, soil features) (Punchi-
476 Manage et al., 2013) or by clustering processes caused by dispersal syndromes or by
477 species interactions (Seidler and Plotkin, 2006; Wiegand et al., 2007).
478

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486 secos: herramientas para su conservación y para el uso sostenible de especies
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References

Asner, G.P., Knapp, D.E., Broadbent, E.N., Oliveira, P.J., Keller, M., Silva, J.N., 2005. Selective logging in the Brazilian Amazon. Science 310, 480–482.

Baddeley, A., Turner, R., 2005. Spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. 12, 1–42.

Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J.-F., Nicolini, E.A., Sabatier, D., 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. J. Appl. Ecol. 49, 861–870.

Berry, N.J., Phillips, O.L., Ong, R.C., Hamer, K.C., 2008. Impacts of selective logging on tree diversity across a rainforest landscape: The importance of spatial scale. Landsc. Ecol. 23, 915–929.

Bjørnstad, O.N., Falck, W., 2001. Nonparametric spatial covariance functions: Estimation and testing. Environ. Ecol. Stat. 8, 53–70.

Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. Ecology 66, 682–687.

Bullock, S.H., Mooney, H.A., Medina, E., 1995. Seasonally Dry Tropical Forests. Cambridge University Press.

Ceccon, E., Huante, P., Rincón, E., 2006. Abiotic factors influencing tropical dry forests regeneration. Braz. Arch. Biol. Technol. 49, 305–312.

Chazdon, R.L., Pearcy, R.W., Lee, D.W., Fetcher, N., 1996. Photosynthetic responses of tropical forest plants to contrasting light environments, in: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Springer US, pp. 5–55.

Clark, J.A., Covey, K.R., 2012. Tree species richness and the logging of natural forests: A meta-analysis. For. Ecol. Manage. 276, 146–153. doi:10.1016/j.foreco.2012.04.001

Comita, L.S., Engelbrecht, B.M.J., 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90, 2755–2765.

Condit, R., Engelbrecht, B.M.J., Pino, D., Pérez, R., Turner, B.L., 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proc. Natl. Acad. Sci. 110, 5064–5068.

Denslow, J.S., 1980. Gap partitioning among tropical rainforest trees. Biotropica 12, 47–55.

Diggle, P., 1985. A Kernel method for smoothing point process data. J. R. Stat. Soc. Ser. C Appl. Stat. 34, 138–147.

Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. Ann. Rev. Env. Res. 28, 137–167.

DongKai, S., DaPao, Y., Li, Z., XiaoKui, X., ZhengGang, L., LiMin, D., 2010. Differences in the structure, species composition and diversity of primary and harvested forests on Changbai Mountain, Northeast China. J. For. Sci. 56, 285–293.

Duclos, V., Boudreau, S., Chapman, C.A., 2013. Shrub cover influence on seedling growth and survival following logging of a tropical forest. Biotropica 45, 419–426.

536 Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L.,
537 Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in
538 tropical forests. Nature 447, 80–82.
539 Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N.,
540 Nielsen, A., Sibert, J., 2012. AD Model Builder: using automatic differentiation
541 for statistical inference of highly parameterized complex nonlinear models.
542 Optim. Methods Softw. 27, 233–249.
543 Fredericksen, T.S., Mostacedo, B., 2000. Regeneration of timber species following
544 selection logging in a Bolivian tropical dry forest. For. Ecol. Manage. 131, 47–
545 55.
546 Fredericksen, T.S., Pariona, W., 2002. Effect of skidder disturbance on commercial tree
547 regeneration in logging gaps in a Bolivian tropical forest. For. Ecol. Manage.
548 171, 223–230.
549 Fredericksen, T.S., Putz, F.E., 2003. Silvicultural intensification for tropical forest
550 conservation. Biodivers. Conserv. 12, 1445–1453.
551 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A.,
552 Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E., 2011. Primary forests are
553 irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.
554 Grogan, J., Galvão, J., 2006. Factors Limiting Post-logging Seedling Regeneration by
555 Big-leaf Mahogany (Swieteniamacrophylla) in Southeastern Amazonia, Brazil,
556 and Implications for Sustainable Management1. Biotropica 38, 219–228.
557 Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the
558 importance of the regeneration niche. Biol. Rev. 52, 107–145.
559 Gullison, R. E., Panfil, S. N., Strouse, J. J., Hubbell, S. P. 1996. Ecology and
560 management of mahogany (*Swieteniamacrophylla* King) in the Chimanes
561 Forest, Beni, Bolivia. Bot. J. Linn. Soc. 122, 9–34.
562 Johns, A.D., 1985. Selective logging and wildlife conservation in tropical rain-forest:
563 Problems and recommendations. Biol. Conserv. 31, 355–375.
564 Johns, A.D., 1988. Effects of "Selective" Timber Extraction on Rain Forest Structure
565 and Composition and Some Consequences for Frugivores and Folivores.
566 Biotropica 20, 31–37.
567 Justiniano, M.J., Fredericksen, T.S., 2000. Phenology of tree species in Bolivian dry
568 forests. Biotropica 32, 276–281.
569 Kelsall, J.E., Diggle, P.J., 1995. Kernel estimation of relative risk. Bernoulli 1, 3–16.
570 Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S., Morales, F., 2002. Effect of
571 disturbance intensity on regeneration mechanisms in a tropical dry forest. For.
572 Ecol. Manage. 162, 197–208.
573 Killeen, T.J., Chavez, E., Pe\ na-Claros, M., Toledo, M., Arroyo, L., Caballero, J.,
574 Correa, L., Guillén, R., Quevedo, R., Saldias, M. et al. 2006. The Chiquitano dry
575 forest, the transition between humid and dry forest in eastern lowland Bolivia.
576 Neotropical Savannas Seas. Dry For. Plant Divers. Biogeogr. Conserv. 213.
577 Killeen, T.J., Jardim, A., Mamani, F., Nelson Rojas, 1998. Diversity, composition and
578 structure of a tropical semideciduous forest in the Chiquitania region of Santa
579 Cruz, Bolivia. J. Trop. Ecol. 14, 803–827.
580 Lebrija-Trejos, E., Bongers, F., Pérez-García, E.A., Meave, J.A., 2008. Successional
581 change and resilience of a very dry tropical deciduous forest following shifting
582 agriculture. Biotropica 40, 422–431.
583 McLaren, K.P., McDonald, M.A., 2005. Seasonal Patterns of Flowering and Fruiting in
584 a Dry Tropical Forest in Jamaica1. Biotropica 37, 584–590.

585 Mendivelso, H.A., Camarero, J.J., Obregón, O.R., Gutiérrez, E., Toledo, M., 2013.
586 Differential growth responses to water balance of coexisting deciduous tree
587 species are linked to wood density in a Bolivian tropical dry forest. PloS One 8,
588 e73855.
589 Merry, F., Soares-Filho, B., Nepstad, D., Amacher, G., Rodrigues, H., 2009. Balancing
590 Conservation and Economic Sustainability: The Future of the Amazon Timber
591 Industry. Environ. Manage. 44, 395–407.
592 Miller, P.M., Kauffman, J.B., 1998. Seedling and sprout response to slash-and-burn
593 agriculture in a tropical deciduous forest. Biotropica 30, 538–546.
594 Mostacedo, B., Putz, F.E., Fredericksen, T.S., Villca, A., Palacios, T., 2009.
595 Contributions of root and stump sprouts to natural regeneration of a logged
596 tropical dry forest in Bolivia. For. Ecol. Manage. 258, 978–985.
597 Münzbergová, Z., Herben, T., 2005. Seed, dispersal, microsite, habitat and recruitment
598 limitation: identification of terms and concepts in studies of limitations.
599 Oecologia 145, 1–8.
600 Murphy, P.G., Lugo, A.E., 1986. Ecology of Tropical Dry Forest. Ann. Rev. Ecol. Syst.
601 17, 67–88.
602 Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.., Kent, J., 2000.
603 Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
604 Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their
605 determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285.
606 Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. Wiley.
607 Panfil, S.N., Gullison, R.E., 1998. Short term impacts of experimental timber harvest
608 intensity on forest structure and composition in the Chimanes Forest, Bolivia.
609 For. Ecol. Manag. 102, 235–243.
610 Park, A., Joaquin Justiniano, M., Fredericksen, T.S., 2005. Natural regeneration and
611 environmental relationships of tree species in logging gaps in a Bolivian tropical
612 forest. For. Ecol. Manage. 217, 147–157.
613 Parker III, T.A., Gentry, A.H., Foster, R.B., 1995. The Lowland Dry Forests Of Santa
614 Cruz, Bolivia: A Global Conservation Priority. Conservation International Rapid
615 Assessment Program, Conservation International, Washington DC, USA.
616 Peña-Claros, M., Peters, E.M., Justiniano, M.J., Bongers, F., Blate, G.M., Fredericksen,
617 T.S., Putz, F.E., 2008. Regeneration of commercial tree species following
618 silvicultural treatments in a moist tropical forest. For. Ecol. Manag. 255, 1283–
619 1293.
620 Pennington, T., Lewis, G.P., Ratter, J.A., 2006. Neotropical savannas and seasonally
621 dry forests: plant diversity, biogeography, and conservation. CRC PressILlc.
622 Pereira Jr., R., Zweede, J., Asner, G.P., Keller, M., 2002. Forest canopy damage and
623 recovery in reduced-impact and conventional selective logging in eastern Para,
624 Brazil. For. Ecol. Manag. 168, 77–89.
625 Poorter, L., 2007. Are species adapted to their regeneration niche, adult niche, or both?
626 Am. Nat. 169, 433–442.
627 Poorter, L., Bongers, L., Bongers, F., 2006. Architecture of 54 moist-forest tree species:
628 traits, trade-offs, and functional groups. Ecology 87, 1289–1301.
629 Poorter, L., Kitajima, K., Mercado, P., Chubiña, J., Melgar, I., Prins, H.H.T., 2010.
630 Resprouting as a persistence strategy of tropical forest trees: relations with
631 carbohydrate storage and shade tolerance. Ecology 91, 2613–2627.
632 Poorter, L., Markesteijn, L., 2008a. Seedling traits determine drought tolerance of
633 tropical tree species. Biotropica 40, 321–331.

634 Poorter, L., Markesteijn, L., 2008b. Seedling traits determine drought tolerance of
635 tropical tree species. Biotropica 40, 321–331.
636 Powers, J.S., Becknell, J.M., Irving, J., Pérez-Aviles, D., 2009. Diversity and structure
637 of regenerating tropical dry forests in Costa Rica: Geographic patterns and
638 environmental drivers. For. Ecol. Manage. 258, 959–970.
639 Pulido, F., García, E., Obrador, J.J., Moreno, G., 2010. Multiple pathways for tree
640 regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers
641 into management schemes. J. Appl. Ecol. 47, 1272–1281.
642 Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Gunatilleke, C.V.,
643 Gunatilleke, I. A. U., Wiegand, K., Huth, A., 2013. Effects of topography on
644 structuring local species assemblages in a Sri Lankan mixed dipterocarp forest.
645 J. Ecol. 101, 149–160.
646 R Core Team, 2013. R: a language and environment for statistical computing. R
647 Foundation for Statistical Computing, Vienna, Austria [WWW Document]. URL
648 http://www.R-project.org/
649 Rother, D.C., Jordano, P., Rodrigues, R.R., Pizo, M.A., 2013. Demographic bottlenecks
650 in tropical plant regeneration: A comparative analysis of causal influences.
651 Perspect. Plant Ecol. Evol. Syst. 15, 86–96.
652 Rozendaal, D.M.A., Hurtado, V.H., Poorter, L., 2006. Plasticity in leaf traits of 38
653 tropical tree species in response to light; relationships with light demand and
654 adult stature. Funct. Ecol. 20, 207–216. doi:10.1111/j.1365-2435.2006.01105.x
655 Seidler, T.G., Plotkin, J.B., 2006. Seed Dispersal and Spatial Pattern in Tropical Trees.
656 PLoSBiol 4, e344.
657 Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B., 2012. Generalized
658 linear mixed models using AD model builder. R Package Version 07 2.
659 Stumpf, K., 2008. The GRS Densitometer. Geographic Resource Solutions, Arcata,
660 USA. <http://www.grsgis.com/publications/densdocumentation2008.pdf>.
661 Verburg, R., van Eijk-Bos, C., 2003. Effects of selective logging on tree diversity,
662 composition and plant functional type patterns in a Bornean rain forest. J. Veg.
663 Sci. 14, 99–110.
664 Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., JC, L., Leaño, C., Pariona,
665 W., Choque, U., 2009. Silvicultural treatments enhance growth rates of future
666 crop trees in a tropical dry forest. For. Ecol. Manage. 258, 971–977.
667 Villela, D.M., Nascimento, M.T., de Aragão, L.E.O.C., Da Gama, D.M., 2006. Effect of
668 selective logging on forest structure and nutrient cycling in a seasonally dry
669 Brazilian Atlantic forest. J. Biogeogr. 33, 506–516.
670 Wiegand, T., Gunatilleke, S., Gunatilleke, N., Okuda, T., 2007. Analyzing the spatial
671 structure of a Sri Lankan tree species with multiple scales of clustering. Ecology
672 88, 3088–3102.
673 Windsor, D. M. 1990. Climate and Moisture Variability in a Tropical Forest: Long-term
674 Records from Barro Colorado Island, Panamá. Smithsonian Contributions to the
675 Earth Science. Washington DC, USA.
676 Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species
677 coexistence. Oecologia 130, 1–14.
678 Wright, S.J., 2010. The future of tropical forests. Ann. N. Y. Acad. Sci. 1195, 1–27.
679 Wright SJ, Jaramillo MA, Pavon J, Condit R, Hubbell SP, Foster RB. 2005.
680 Reproductive size thresholds in tropical trees: variation among individuals,
681 species and forests. J. Trop. Ecol. 21, 307–315.
682 Zuur, A.F., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer.

683 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid
684 common statistical problems. Methods Ecol. Evol. 1, 3–14.
685 Zuur, A.F., Saveliev, A.A., Ieno, E.N., 2012. Zero inflated models and generalized
686 linear mixed models with R. Highland Statistics Ltd., Newburgh, U.K.
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688
689 **Tables**

690

691 **Table 1.** Logging microsites described by mean values of variables measured to
692 characterize them. The χ^2 statistics correspond to Kruskal-Wallis tests based on multiple
693 comparisons between microsites performed for each variable. For Area, a Wilcoxon-
694 rank test was used. Different uppercase letters indicate that mean variables significantly
695 differed between microsites. Significance levels: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

	Microsites					
Variables (units)	log landings	logging roads	skid trails	logging gaps	undisturbed	χ^2
Length (m)	34.16^{a}	4.83^{b}	3.71^{c}	13.54^{d}	---	69.51^{***}
Area (m^2)	1165.68^{a}	---	---	129.12^{b}	---	---
Trees (%)	3.17^{a}	36.09^{a}	70.21^{b}	21.30^{b}	81.25^{c}	69.29^{***}
Shrubs (%)	37.13^{a}	26.48^{a}	20.33^{ab}	39.78^{bc}	42.92^{c}	17.34^{**}
Woody vines (%)	9.04^{a}	4.70^{ab}	7.33^{abc}	10.91^{bc}	20.54^{c}	10.45^{*}
Herbaceous vines (%)	7.25^{a}	6.48^{a}	15.96^{ab}	18.13^{bc}	10.13^{c}	17.15^{**}
Herbs (%)	1.58^{a}	1.04^{a}	4.75^{ab}	6.04^{bc}	4.29^{c}	16.85^{**}
Canopy openness (%)	62.06^{a}	37.29^{a}	14.01^{c}	28.13^{d}	4.38^{e}	88.54^{***}
Soil water content (%)	19.22^{a}	16.76^{ab}	17.22^{ab}	16.19^{ab}	15.02^{b}	3.58^{**1}
Soil compaction (N m^{-2})	362.81^{a}	342.41^{a}	174.06^{b}	144.07^{bc}	151.44^{c}	76.33^{***}

696 [1]This statistic corresponds to the *F* value of an ANOVA and a Tukey post-hoc test.

697

698 **Table 2.** The five most abundant species with guilds and the observed seedling and
699 resprout density. Values are means ± SE.

Species	Guild	Seedling density (ind. m^{-2})	Resprout density (ind. m^{-2})
Acosmium cardenasii	shade-tolerant	0.341 ± 0.052	0.194 ± 0.052
Anadenanthera macrocarpa	long-lived pioneer	0.097 ± 0.024	–
Astronium urundeuva	long-lived pioneer	0.025 ± 0.019	–
Caesalpinia pluviosa	partially shade-tolerant	0.049 ± 0.016	0.027 ± 0.009
Machaerium acutifolium	partially shade-tolerant	0.25 ± 0.1340	0.021± 0.007

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Table 3. Main results of the zero-inflated Poisson mixed models showing their ranking and the relative importance of variables explaining the abundance of seedlings of the most abundant tree species. The symbol "✓" indicates that the corresponding variable entered that model. Variables abbreviations are: COPEN, canopy openness; SCOMP, soil compaction; SWC, soil water content; RESPA, resprout abundance; SDD, density of short-distance dispersal "mother" trees; LDD, density of long-distance dispersal "mother" trees. The ranking of the models according to their parsimony was based on the Akaike Information Criterion (AIC) and Akaike weights (*Wi*). The relative importance of a variable is the sum of the *Wi* of all models including that variable.

Species	**Rank**	**COPEN**	**SCOMP**	**SWC**	**SDD**	**LDD**	**AIC**	***Wi***
Acosmium cardenasii	1	✓	✓				338.070	0.583
	2	✓	✓	✓			339.994	0.223
	3		✓				340.924	0.140
	4		✓	✓			342.850	0.053
Relative importance		**0.806**	**0.999**	**0.276**				
Anadenanthera macrocarpa	1	✓			✓		169.663	0.261
	2	✓	✓			✓	170.130	0.206
	3	✓	✓		✓		170.462	0.175
	4	✓		✓	✓		171.387	0.110
	5	✓	✓	✓		✓	171.575	0.100
	6	✓	✓	✓	✓		171.672	0.095
Relative importance		**0.948**	**0.577**	**0.306**	**0.641**	**0.307**		
Astronium urundeuva	1					✓	39.009	0.328
	2	✓				✓	40.454	0.160
	3			✓		✓	40.685	0.141
	4		✓			✓	40.997	0.121
	5	✓					41.314	0.103
	6	✓		✓		✓	41.846	0.080
	7	✓	✓				42.189	0.067
Relative importance		**0.409**	**0.067**	**0.221**	**0**	**0.829**		
Caesalpinia pluviosa	1	✓	✓		✓		102.577	0.336
	2	✓	✓			✓	103.758	0.186
	3	✓	✓	✓	✓		104.503	0.128
	4	✓	✓	✓		✓	105.625	0.073
	5	✓				✓	106.087	0.058
	6	✓	✓				106.179	0.055
	7		✓				107.027	0.036
	8	✓		✓		✓	107.997	0.022
	9		✓			✓	108.034	0.022
	10	✓	✓	✓			108.159	0.021
	11		✓		✓		108.630	0.016
Relative importance		**0.880**	**0.874**	**0.244**	**0.480**	**0.362**		
Machaerium acutifolium	1	✓					225.428	0.531

	2	✓	✓		227.404	0.198
	3	✓		✓	227.410	0.197
	4	✓	✓	✓	229.390	0.073
Relative importance		**0.999**	**0.271**	**0.270**		

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714 **Table 4.** Parameters of the most parsimonious fitted Zero-Inflated Poison Mixed
715 Models for seedling establishment of the five most abundant tree species. Soil water
716 content was not significant in the best-fitted models. Significance levels are indicated as
717 in Table 1 and variables abbreviations are as in Table 3.

718

Species	intercept	COPEN	SCOMP	SDD	LDD
A. cardenasii	-0.13	-0.42*	-1.07***	–	–
A. macrocarpa	0.22	0.94***	–	0.41**	
A. urundeuva	-1.87	–	–	–	1.26***
C. pluviosa	-4.39***	-1.97*	-1.82*	0.70*	–
M. acutifolium	-1.79***	-1.31***	–	–	–

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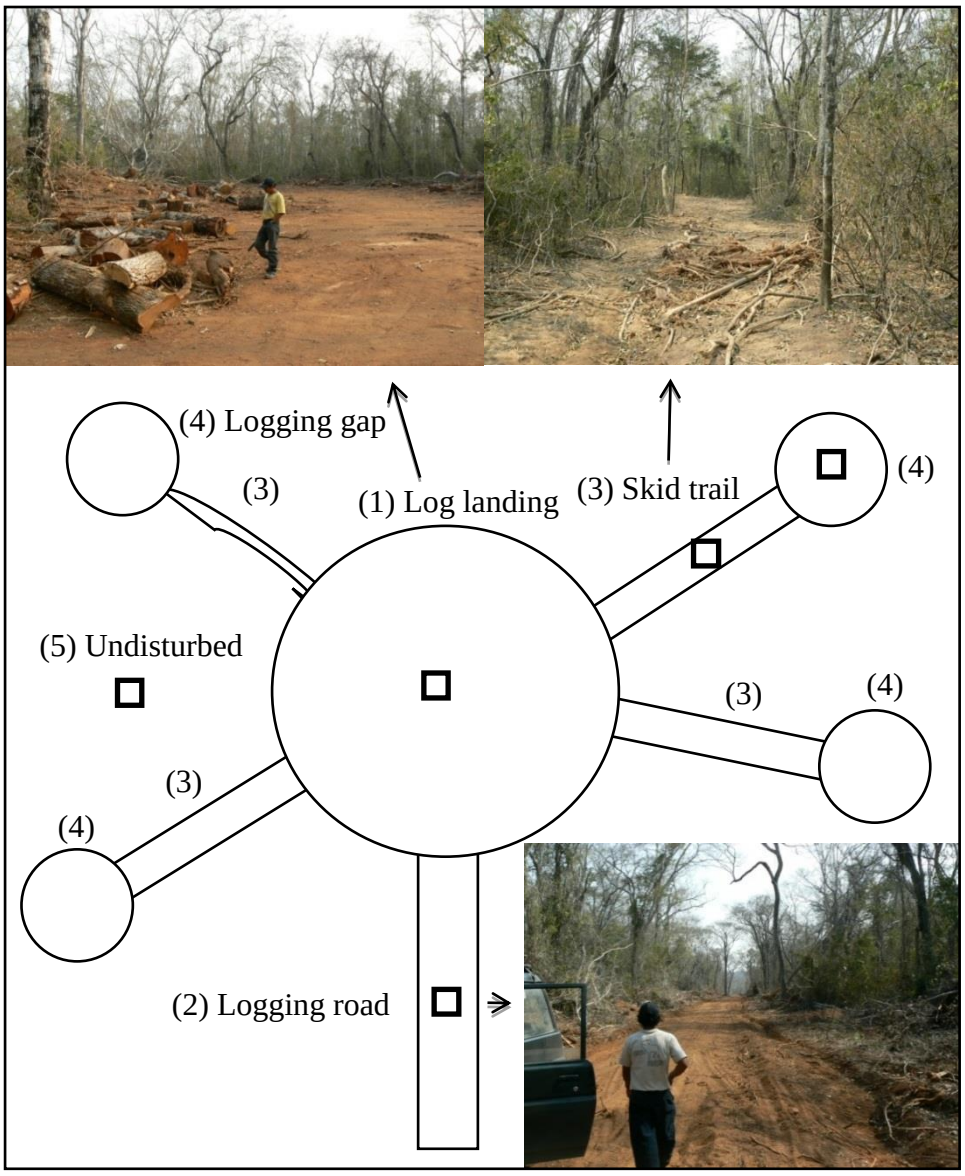
726 **Figures**



727

728 **Figure 1.** Overview of the sampling design and illustrations of log landing, skid trails
729 and logging road.

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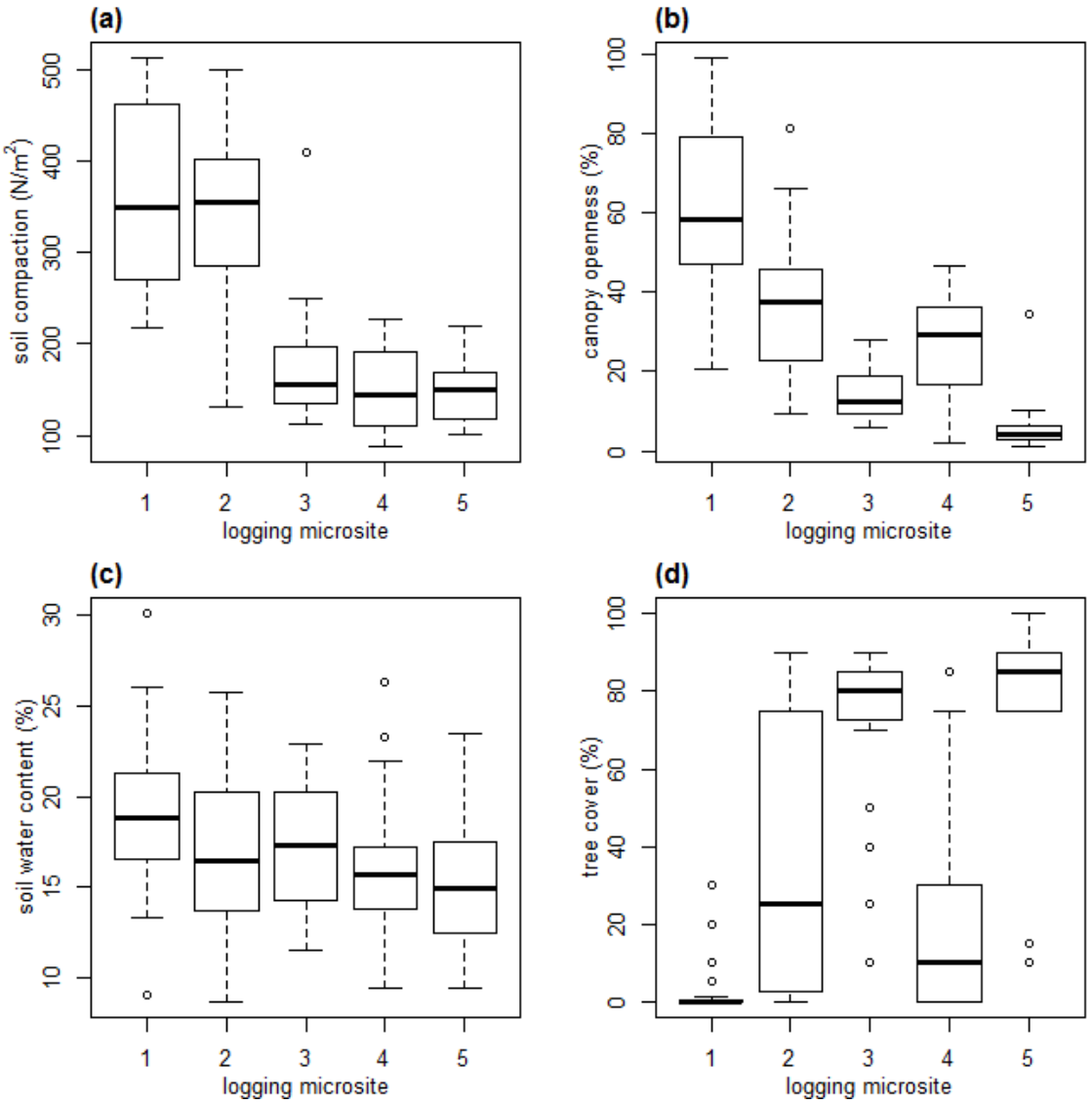

Figure 2. Boxplots showing the variability of variables measured in logging microsites: a, soil compaction; b, canopy openness; c. soil water content; d, tree cover. Logging microsites are indicated by numbers as in Figure 1 (1, log landing; 2, logging road; 3, skid trail; 4, logging gap; 5, undisturbed forest).

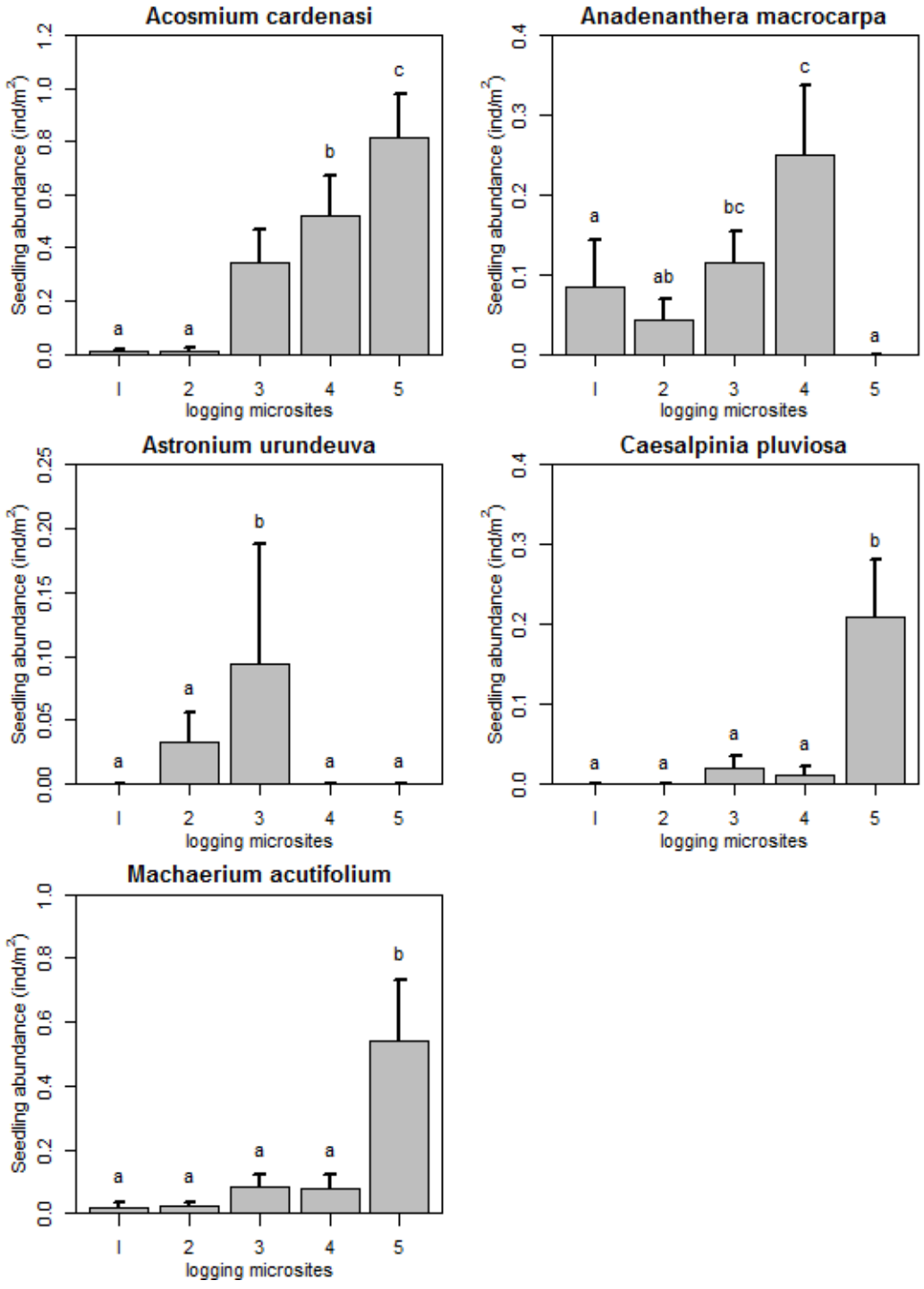

Figure 3. Mean seedling abundances of the studied tree species in each logging microsite. Error bars are standard errors. Different letters over bars indicate significant differences (P<0.05) according to Kruskal-Wallis tests used for doing multiple comparisons among microsites. Logging microsites are indicated by numbers as in Figure 1 (1, log landing; 2, logging road; 3, skid trail; 4, logging gap; 5, undisturbed forest).

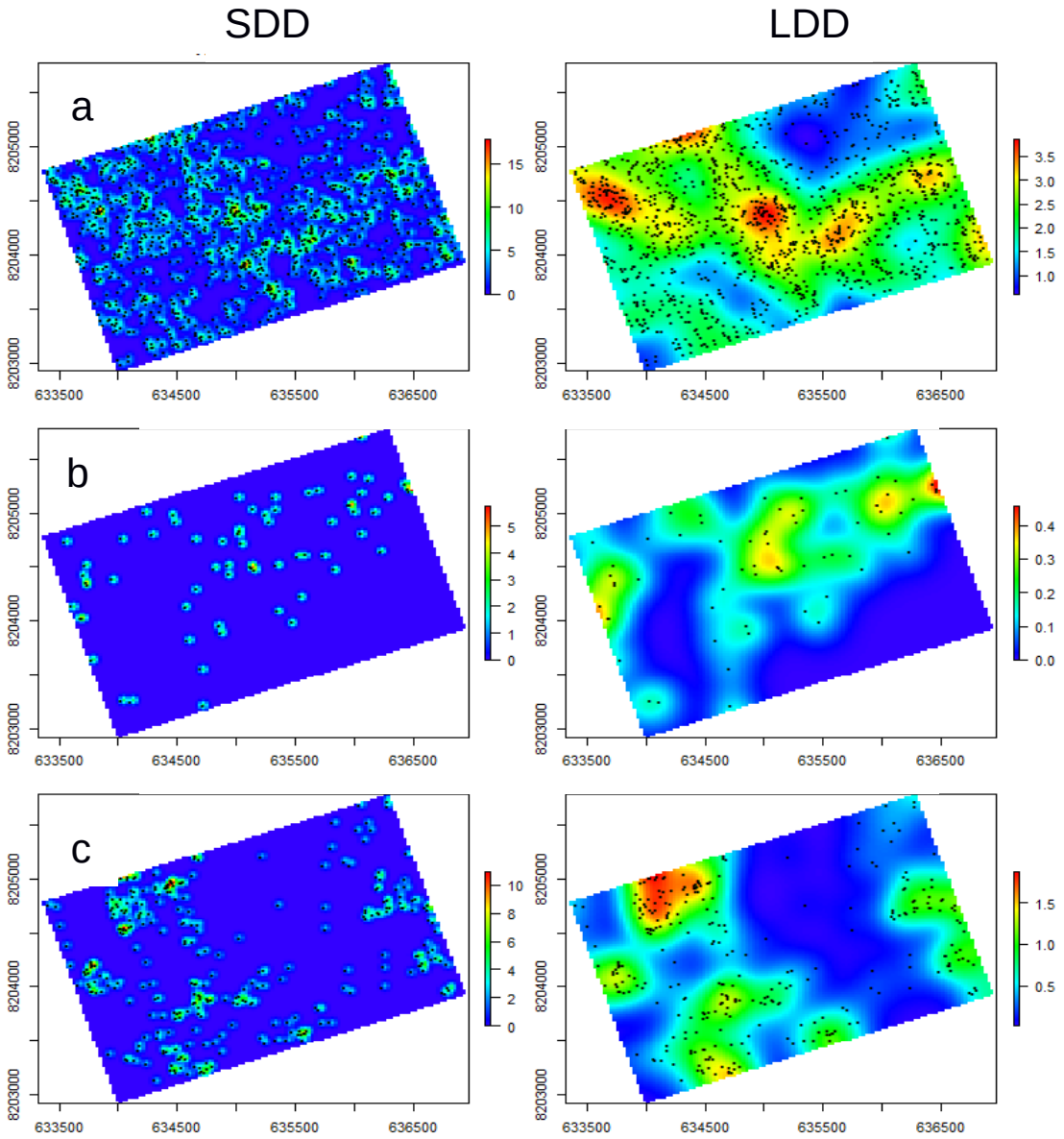

Figure 4. Kernel maps showing interpolated tree density data (ind ha^{-1}, color scales) with locations of adult individuals of three canopy trees (a, *Anadenanthera macrocarpa*; b, *Caesalpinia pluviosa*; c, *Astronium urundeuva*) in the first study area. The two columns show different bandwidth selection methods used to estimate tree density as a surrogate of short- (SDD, left column) and long-distance seed dispersal (LDD, right column), respectively. The *x* and *y* axes correspond to UTMX and UTMY coordinates, respectively.

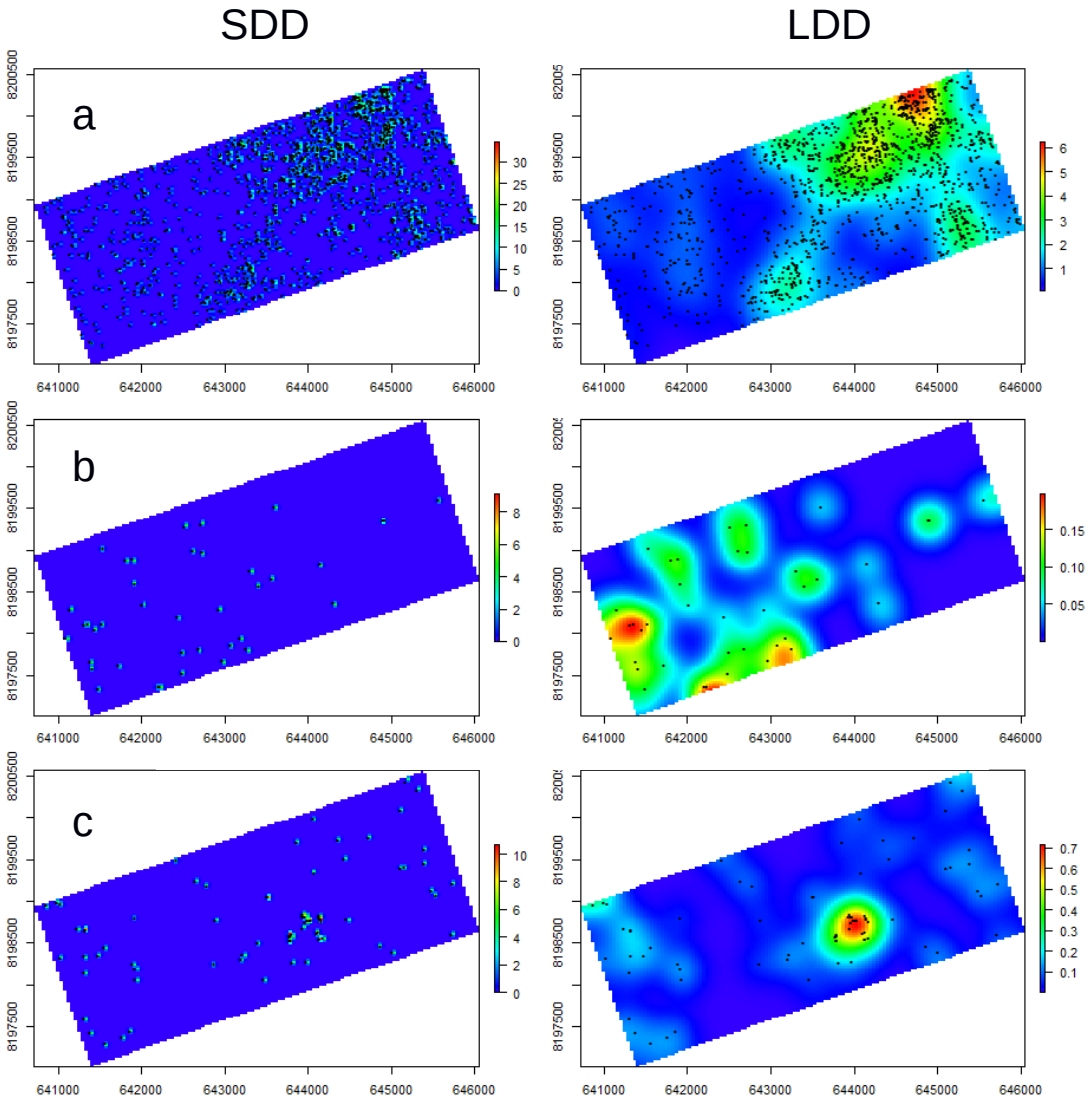

Figure 5. Kernel maps showing interpolated tree density data (ind ha^{-1}, color scales) with locations of adult individuals of three canopy trees (a, *Anadenanthera macrocarpa*; b, *Caesalpinia pluviosa*; c, *Astronium urundeuva*) in the second study area (1000 ha). The rest of explanations are as in Figure 4.

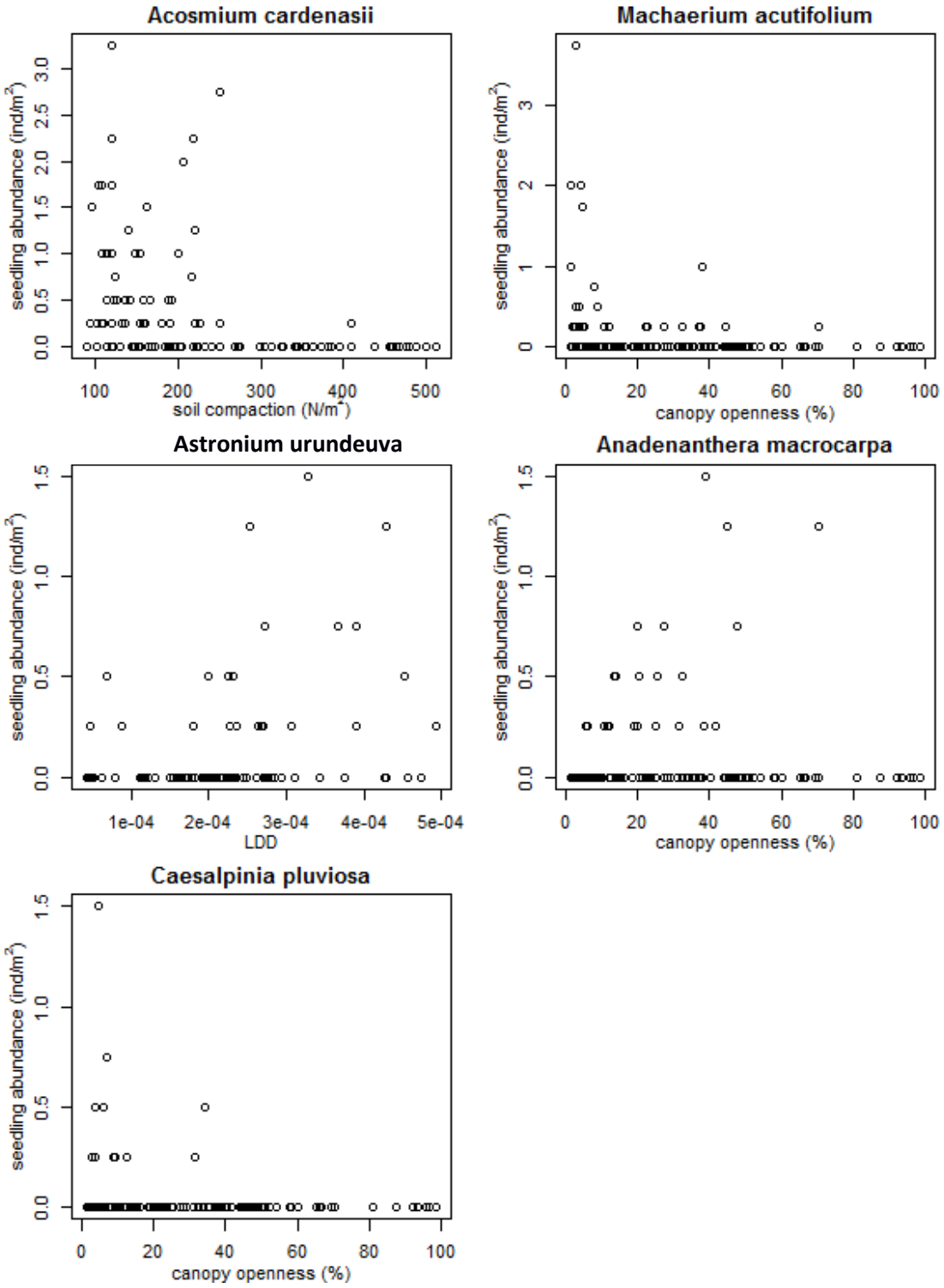

Figure 6. Scatter plots showing seedling density of selected tree species as related to the main explanatory variables revealed by the Zero-Inflated Poison Mixed Models (see Tables 3 and 4). SDD and LDD refer to short- and long-distance seed dispersal, respectively.